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Abstract

It is still largely unknown what effect does wolf risk have on the lower trophic levels in Europe. In the last European lowland forest these interactions were explored with a main browser species – red deer (*Cervus elaphus*), and other four less common ungulate species, one of which is European bison (*Bison bonasus*). To explore the effect of risk I use community-averaged and species-specific plant traits as indicators in regenerating tree communities. Browsing intensity and several functional plant traits were related to relative wolf (*Canis lupus*) encounter risk, red deer and other ungulate biomasses, and horizontal visibility factors. Browsing intensity did not decrease even in the areas where wolf encounter rate is high and red deer biomass is low. Evidence points out that bison could be as important browser in a deciduous mixed forest as red deer is. The full height of saplings and the height of the first branch mainly depended on red deer biomass. The height of the fork and branching index related more to other ungulate biomass and horizontal visibility. While coexisting in the same forest but on the opposite ends of wolf predation risk, the two browsers may be important top-down drivers within the system.

Keywords: red deer, wolf, bison, browsing, plant traits, landscape of fear

Contents

Introduction

Since the 1960s contrasting views of bottom-up and top-down vegetation control have been swaying from one side to the other (Gordon and Prins, 2008). In this case "bottom-up" refers to a resource-controlled system such as water, nutrient and light availability (Bond, 2005). It also implies that plants can control the amount of damage by producing defenses (Drent and Prins, 1987). There is no doubt that herbivores play an important role in ecology (Estes *et al*., 2011). In addition, Hairston *et al* (1960) suggested that herbivores are more limited by predators than by food, giving rise to "green world hypothesis". However, even with over 50 years of research main ecosystem drivers have not yet been identified for many specific systems (Churski *et al*., 2016). Recently published research suggest that top-down vegetation control may have a bigger role than previously thought (Estes *et al*., 2011) and herbivores may be very successful at controlling resource-rich parts (Churski *et al*., 2016). Polis (1999) has argued that herbivores cannot reduce plant biomass enough to be the main force of ecosystem. However, the scale matters, and when looking at a specific system, finer properties should be considered (Staver *et al*., 2012). Now, a widely accepted consensus has been reached that terrestrial ecosystems are a finely detailed mosaic of bottom-up and top-down forces occurring simultaneously (Turkington, 2009). Gripenberg and Roslin (2007) also argues that these forces may become stronger or weaker depending on space and time. As there are more interaction than just vertical, conservative views of top-down and bottom-up vegetation control may be limiting our understanding of biome formation.

Bond (2005) suggested that considering fire and herbivory, in addition to climate and soils, may lead to better, more functional, definitions of biomes. Fire has always been regarded as consumer control alongside herbivory. Yet, studies that looked into these forces as separate drivers for biome formation distinguish them (Staver *et al*., 2012; Charles-Dominique *et al*., 2015). Bond (2005) provided evidence that certain world biomes could have only formed due to fire regimes. Fire generally removes grassy build-up (Charles-Dominique *et al*, 2015), and depending on intensity can remove

shrublands (Bond, 2015). Herbivory alone cannot reduce a significant amount of biomass, it can only be done in a combination of herbivory and fire (Staver *et al*., 2009). Yet herbivory still influence plant ecology and formation. Mesoherbivores have been shown to have influence on limiting tree recruitment, changing tree composition, creating browsing lawns and affecting functional plant traits (Staver and Bond, 2014; Churski *et al*., 2016). Bond introduced the terms green, black and brown world to conceptualize plant communities driven by climate, fire and herbivory as selection pressures respectively.

An attempt of recognising fine features of herbivory and fire-controlled plants was made by several studies. While the green world patches have been identified by temperature and precipitation, which explains major global biomes (Holdridge, 1974). There is no consensus on how to identify brown and black world patches (Bond, 2015), Charles-Dominique *et al*. (2015) attempted to separate biomes by using functional plant traits. Charles-Dominique *et al*. (2015) study observed plant traits under the same environmental conditions, however, vegetation types showed to be extremely different. Tolerance to browsing and to fire can be phenotypically expressed by plant traits (Diaz *et al*., 2007; Pausas *et al*., 2004), and can vary widely in their expression depending on which force is more dominant. Such differences can be observed in branching architecture, bud protection, bark thickness, specific leaf area, seed mass and size, root:shoot ration and other traits (Westoby *et al*., 1996; Hoffman *et al*., 2004; Wigley *et al*., 2014; Charles-Dominique *et al*., 2015). Indications were made towards browsing being limited by the structure of the whole-plant (Charles-Dominique *et al*., 2017). This type of protection was described for *Acacia* species several times (Charles-Dominique *et al*., 2017) but never for any species in temperate forest system. In the same environment *Acacia karoo* can develop a "cage" structure and "pole" structure as a response to browsing or fire disturbance (Archibald *et al*., 2003). "Pole" structured trees have tall and thin trunk with low branching density, alternatively, "cage" structure has wide, highly branched

canopy (Archibald *et al*., 2003). Fire history in Białowieża Primeval Forest shows that fires were part of the ecosystem in 1800s in coniferous parts of the forest (Niklasson *et al*., 2010). Since *Carpinus* has expanded in many parts of the forest in the early 90s (Kuijper *et al*., 2010) the fires have not been common. Therefore, the system should be dominated by green and brown world plant species or traits.

Brown world, or herbivory-related, plant traits can be divided into tolerance and avoidance strategies as an evolutionary response to browsing (Skarpe and Hester, 2008). It does not come as a surprise that plants have developed avoidance strategies such as prickles and thorns that prevent herbivory or reduce the bite size (Shipley, 2007; Skarpe and Hester, 2008). Generally, avoidance strategies in plants develop in nutrient-poor environments, while in a nutrient rich environment plants tend to tolerate herbivory (Coley *et al*., 1985). This type of trade-off also has certain costs, as plants must invest more into storing energy to allow the production of buds after an herbivory event (Skarpe and Hester, 2008) thus is only possible in an environment where resources are not limited. Since, temperate forest is a resource rich environment plants can allow themselves to be under high browsing pressure, persevere for longer times and develop brown-world traits (Churski *et al*., 2016). In a system with plentiful resources chronic browsing can create a "browse trap" (Staver and Bond, 2014), an effect similar to "fire trap" where tree height is being diminished by one or both types of disturbance. However, plants held in a "browse trap" can be released by top-down forces such as diseases or predation (Churski *et al*., 2017).

Krebs (2001) suggested that without predator, pest and pathogen control herbivore populations would explode. In Europe the indirect predator impact on plants is rather unexplored. The result of predator control on vegetation has been mainly observed in North America (Kuijper *et al*., 2016(a)). In Europe predators are expanding to areas where they have not been seen for hundreds of years (Chapron *et al*., 2014), however the research on the effect they cause is lagging. Trophic cascades were illustrated well in

Yellowstone national park in the US (Ripple and Larsen, 2000; Ripple *et al*., 2001; Beschta 2003), such powerful effects have not been observed in Białowieża, but a three-level trophic interaction has been (Kuijper *et al*., 2013). Browsing intensity was shown to be affected by the presence of wolves in high risk areas (Kuijper *et al*., 2013). On the other hand, there are numerous of studies showing that in largely human dominated landscape the effect of predation is far lesser than in Yellowstone (Kuijper *et al*., 2016(a); Kuijper *et al*., 2016(b); Allen *et al*., 2017; Zbyryt *et al*., 2017). Thus, the effect of fear may not be as observable on plants in Europe as has been reported in North American studies.

As the effect of browsers on the formation of functional plant traits are lacking in Europe and never been tied to predation, I aim to explore plant traits in regenerating tree communities throughout predation risk gradient. This study aims to fill in some gaps in knowledge on how functional plant traits could be related to the landscape of fear in a temperate forest system. This thesis was designed to consider following hypotheses:

H1: Browsing intensity on regenerating trees varies depend on perceived risk.

H2: Brown-world functional plant traits differ within the forest depending on perceived risk factor.

Methods

Study site

The Białowieża national Park (BNP) is a restricted area within Białowieża primeval forest in the eastern part of Poland. BNP is 105.2 km^2 of old-growth forest with minimized human activities. Visitors can only visit the park with a special permit or accompanied by a guide. Neither hunting nor tree felling is permitted in this specific area, which allows to consider the system that is not disturbed by most influential human activities. There is a high variation of soil types in BNP, where the coniferous forest type occurs on poorer soil types, and deciduous and mixed deciduous forest types occur on richer soil types (Bernadzki *et al*., 1998). Deciduous and mixed deciduous forest types dominate the park's landscape (Kuijper *et al*., 2013), and mainly consist of: *Carpinus betula, Tilia cordata, Quercus robur* and *Picea abies* (Bernadzki *et al*., 1998).

Relative density based on drive counts have been estimated in the same way in BNP for the last decades. Data from the 2010 drive count estimated 12 red deer per km^2 in BNP (Kuijper *et al*., 2013). Wild boar (*Sus scrofa*) was until recently second most common ungulate in the area until African Swine Fever entered Poland in February 2014 (Śmietanka *et al*., 2016), after which population in BNP has dramatically decreased by around 80% (Gallardo *et al*., 2015). No recent data is available after the collapse of wild boar population. Data from drive counts also show density of roe deer (*Capreolus capreolus*) was around 2 individuals per km^2, European bison (*Bison bonasus*) – 0.8 individuals per km^2 and moose (*Alces alces*) also occur in 0.4 individuals per km^2.

Grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) are the apex predators in BNP (Schmidt *et al*., 2009). Lynx diet consists mainly of roe deer (Jędrzejewski and Sìdarovìč, 2010), and therefore, it was not considered in the study. Even though wolf occasionally kill other ungulates, red deer and wild boar, before the collapse, are the most common prey items in the park.

One single wolf pack occupied the BNP throughout the year during the study and the years before. As there has not been any hunting in the area, the general pack territory remains unchanged (Jędrzejewski *et al*., 2007), although the core wolf area may change between seasons or even within the season (Schmidt *et al*., 2008).

Study design

Kuijper *et al* (2015) showed that the highest wolf density occurs furthest away from human settlements and the lowest activity can be found the closest to the settlements. I used this finding to divide the study site in three bands at differing distances away human settlements (distance class 0, 1, 2, and 3) (fig 1.). The settlements in my interest area include Białowieża and Pogorzelce villages. Distance class 0 (table 1) is an open meadow habitat outside of the forest habitat which is located the closest to human settlements, however additional data on total ungulate and red deer biomass and wolf density was not available for this distance class. Distance class 1 is a forest habitat closest to human settlements, that also has the highest red deer biomass, and the lowest wolf density. Distance class 2 has smaller numbers of red deer biomass and more relative wolf density than latter distance class (table 1). Distance class 3 is the furthest away to human settlements, it has low red deer biomass and the highest relative wolf density (fig.2) (table 1). Ungulate biomass and wolf density were acquired from an extensive camera trapping study by Bubnicki *et al* (personal communication, 2018) (fig.2). The numbers were calculated for a landscape grid of 25ha from daily camera trap rates during 2 year period (from May, 2012 to May, 2014) (table 2). Total ungulate biomass, red deer biomass and relative wolf density were assigned to the coordinates that fell into the landscape grid system. Every sampling location was given relative estimate of red deer, total ungulate biomass and relative wolf density. I used these variables as covariates in my models. From the total biomass I subtracted red deer biomass to obtain other ungulate biomass, which includes bison, wild boar, roe deer and moose

Table 1. Total ungulate biomass, red deer biomass and wolf density per distance class in 25ha landscape grid during 2 year period.

Distance classes	Distance from settlements (m)	Total ungulate biomass (kg in 25ha)	Red deer biomas (kg in 25ha)	Wolf density (individuals in 25ha)
Distance class 0	<1500m	No data	No data	No data
Distance class 1	1500 - 3000	1350 - 1700	500 - 850	3 - 6
Distance class 2	3000 - 4500	1000 - 1300	250 - 700	7 - 11
Distance class 3	4500 – 6000	1000 - 1300	250 - 450	7 - 11

In each of the three distance classes I laid out five transects (15 in total). Every transect had three sampling locations (45 sampling locations in total, see figure 1). The starting points of these transects were randomly assigned on Geographical Information software (QGIS) before data collection. Points were assigned excluding swampy black alder forest and coniferous forest types. To avoid walking out of the specific distance class starting points were selected roughly in the centre of distance class.

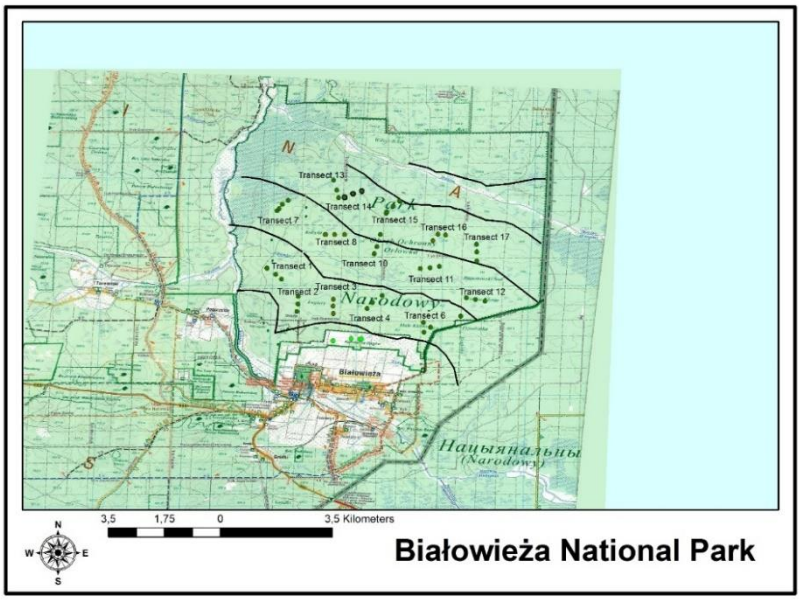

Figure 1. Map of Białowieża National park with sampling sites.

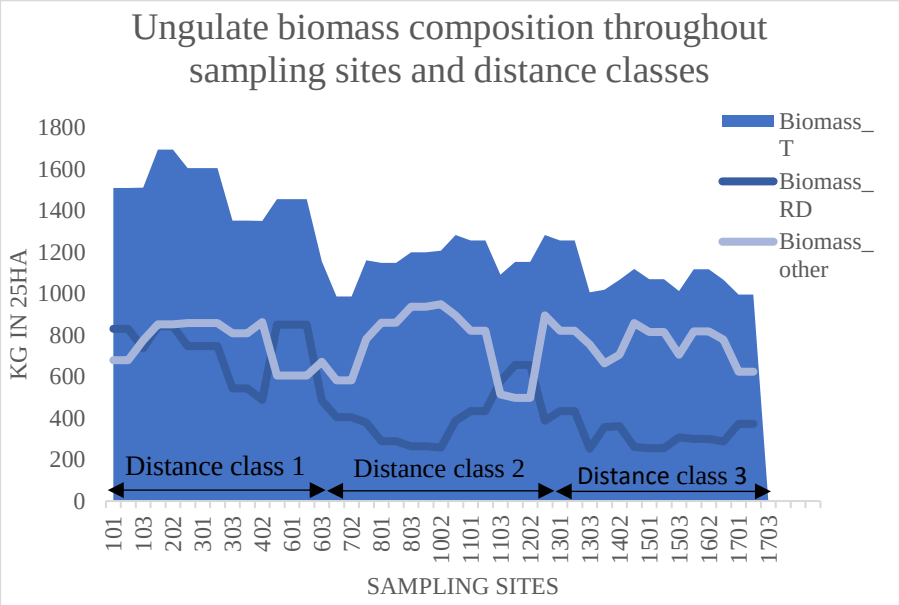

Figure 2. Combination graph for ungulate biomass composition. Biomass_T – total ungulate biomass, biomass_RD – red deer biomass, biomass_other – other ungulate biomass.

Data collection

In each of the 45 sampling locations I recorded 20 individual regenerating trees in a height class from 50cm to 150cm, as browsing was mostly limited to within this range of height (Kuijper *et al.*, 2010). I navigated to the starting locations assigned in ArcMap beforehand. This starting location was also the first sampling plot. I started with marking the middle line of the sampling location with a 25-metre measuring tape (fig. 3). Every woody plant individual within the mentioned height range was included if it was not further than 2 metres away from the middle line. This method enabled to count the area that 20 plants occur in, expand area according to plant density and avoid measuring the same plant twice. The direction of a transect was determined randomly from the middle of the starting location. To choose a cardinal direction randomly I spun around myself and threw a stick to determine the direction of a transect. I walked exactly 250 metres to the direction of a stick to set the second sampling plot. For the third sampling plot I walked another 250 metres the same direction as previously.

A number of plant traits were recorded for all measured woody plant individuals. Every plant was identified by species, when possible, some could to be only narrowed down to genus. I used a telescopic stick with centimetre marks to measure full height, the height from ground up to the highest living foliage (Pérez-Harguindeguy *et al.*, 2013). I recorded height of the first major branch and height of the first fork whenever it was possible with the telescopic stick. I measured stem diameter with calliper 10 centimetres above the ground. I also identified the terminal leading shoot of the main stem to count primary branches (all branches coming from the main stem). Dead primary branches were also included in the count to capture overall plant architecture better. Browsing intensity was measured by counting how many of top 10 branches are missing their shoots (Kuijper *et al.*, 2013).

I measured canopy openness and horizontal visibility at each sampling location as possible drivers of variation in plant traits. I took 180° degree pictures of the canopy with a fisheye lens (Raynox DCR-

CF185PRO) to calculate relative canopy openness. The camera was placed on a tripod and pictures taken with exposure value of 0. Three pictures were taken in most sampling locations: one at the starting location of the 25m line and two from opposite sites of sampling plot. These pictures were later transformed into black and white and white pixels were counted in image retouching program GIMP (The GIMP Development Team). I then transformed this into relative percentage of canopy openness (as the % of white pixels). I also used a handheld rangefinder (Bresser 4 x 21 Range-finder.800) to determine visibility from the start of 25m line. I took a reading with a rangefinder was noted from all four-cardinal direction, later readings were averaged for every plot.

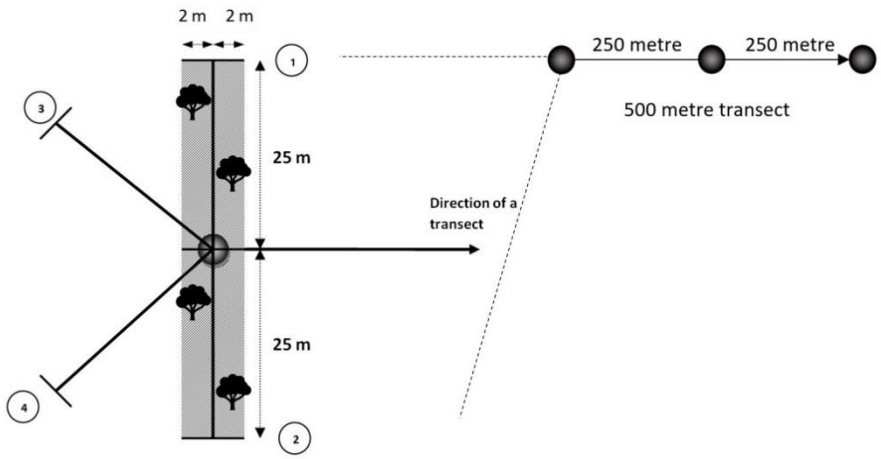

Figure 3. A method of sampling in each transect and each location. Transect on the right and sampling plot on the left. Circle in the centre represents the start of the sampling location. Lines are the centre lines and grey area shows plot.

Statistical analysis

In addition to traits collected in the field I calculated a few additional indices that further reflect plant functional traits. Branching index was calculated by dividing the number of primary branches by the height. Diameter-height index was calculated by dividing the diameter by the full

height. For each of the measured plant traits and indices, I then calculated the average value across the twenty individuals per sampling location level to represent the community weighted mean for each of the traits. I also performed plant species-specific analyses, where I averaged individuals from the same species at a sampling plot level.

The distribution of most of the continuous variables fell into normal distribution according to the Anderson-Darling test. However, the height of the first branch and diameter-height index were not normally distributed. The height of the first branch was transformed with natural logarithm transformation. Diameter-height index was transformed using arcsine transformation.

All statistical tests were performed using R-studio (RStudio, Inc). Analysis of variance (ANOVA) was used to check for differences between the distance classes and between different species across all distance classes. I used variance inflation factor (VIF) to check for multicollinearity (fig.4). Variables that were most correlated (>0.5) were not used as explanatory variables in the same model. Principal component analysis (PCA) was used to identify the strongest explanatory variables (fig.5). First, I looked at the relationship between the community weighted means and explanatory variables for every plant trait. I used ANCOVA in order to make an interaction between a categorical variable (distance class) and continuous variable (ungulate biomass and relative wolf density). Simple models with one continuous explanatory variable (wolf density, red deer biomass, total ungulate biomass, the rest of ungulate biomass, visibility and canopy openness), did not explain the variation in most cases. Models performed much better when either a categorical variable – distance class, or continuous variable – visibility were included.

Second, I looked at the species-specific response in the same manner. Species specific response could only be done for three species – *Carpinus betulus* (Common hornbeam) (n = 475), *Tilia cordata* (Small-leaved lime) (n

= 208) and *Acer platanoides* (Norway maple) (n = 65). I excluded the other species since they did not occur in all distance classes or there were not enough data points. Rest of the species were grouped together (n=152), the group includes species: *Sorbus aucuparia* (Rowan), *Frangula alnus* (Alder buckthorn), *Ulmus glabra* (Scotch elm), *Alnus glutinosa* (Black alder), *Euonymous europaeus* (European spindle), *Quercus robur* (European oak), *Corylus avellana* (Common hazel), *Fraxinus excelsior* (European ash), *Picea abies* (Norway spruce), *Betula spp* (Birch) and *Populus tremula* (European aspen).

Figure 4. Colinearity by variance inflation factor (VIF) for explanatory variables

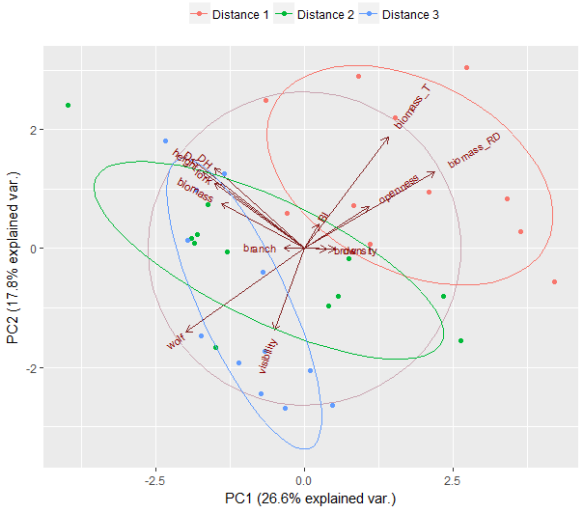

Figure 5. PCA of sampling plots in three distance classes. Distance class 1 is separated from other classes by canopy openness, total ungulate biomass and red der biomass. Distance 2 and 3 have quite a lot of overlap.

Table 2 (was 1). Other ungulate composition with daily trapping rate, standard deviation and percentage of daily trapping rate.

Species	**Trap rate (daily)**	**Trap sd**	**Daily trap rate (%)**
European Bison	0.04	0.23	60.85
Roe Deer	0.02	0.07	27.49
Eurasian Elk	0.01	0.05	11.65

Results

Red deer numbers in distance class 1 were higher than in other two classes ($p<0.001$), yet other ungulate biomass did not vary throughout distance classes ($p=0.877$), and relative wolf density increased throughout distance classes ($p<0.001$) (fig.6). Red deer biomass decreased when it was tested against relative wolf density($p<0,001$) and did not decrease when I tested it against visibility ($p=0.065$) (fig.7). The rest of ungulate biomass increased with increasing relative wolf density ($p=0.019$) and did not change with increased visibility ($p=0.133$) (fig.6).

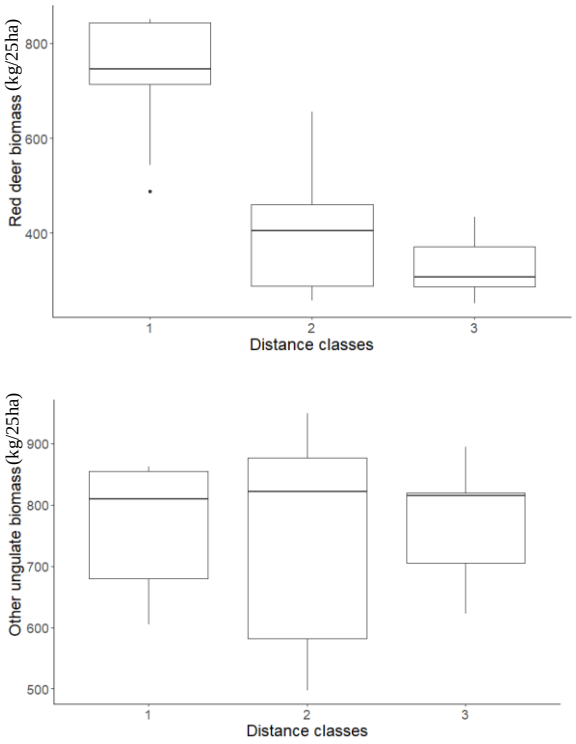

Figure 6. Boxplots showing red deer biomass in kg in 25ha (top) and other ungulate biomass in kg in 25ha (middle) and relative wolf density (bottom) in different distance classes.

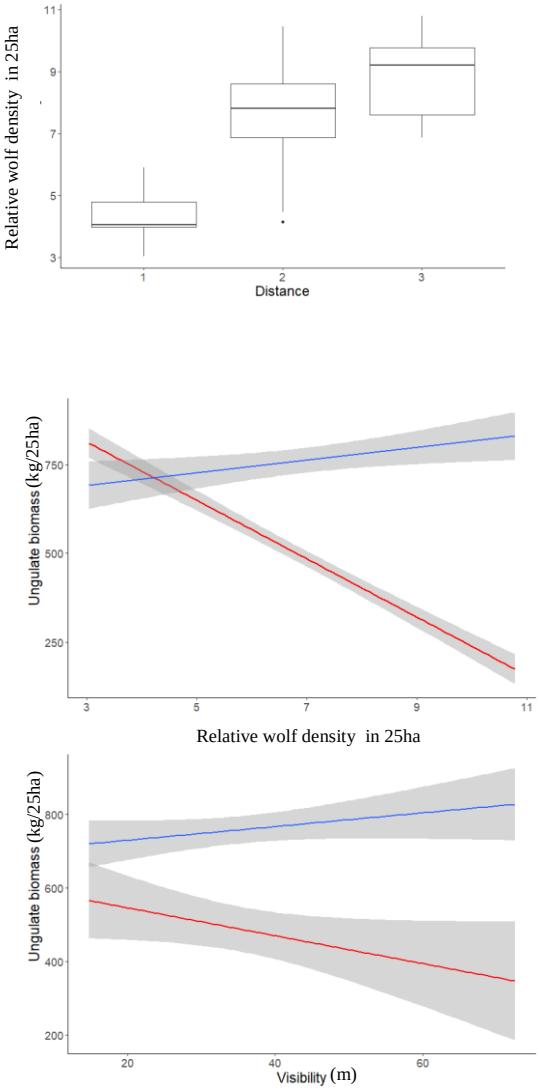

Figure 7. A linear relationship between two different ungulate biomass changes in response to the wolf denstiy on the top. Relationship between two different ungulate biomass changes in response to visibility on the bottom. Red line - red deer biomass, blue line - ungulate biomass (excluding red deer) and 95% confidence interval in grey.

Browsing intensity

Community-averaged response

Average value of browsing intensity did not vary among distance classes (fig.9). Variation in browsing intensity was explain the best by an interaction between visibility and distance (visibility x distance, p=0.003, F=6.827)

(table 3). Browsing intensity increases in distance class 2 and decreases in distance class 3 (fig.8).

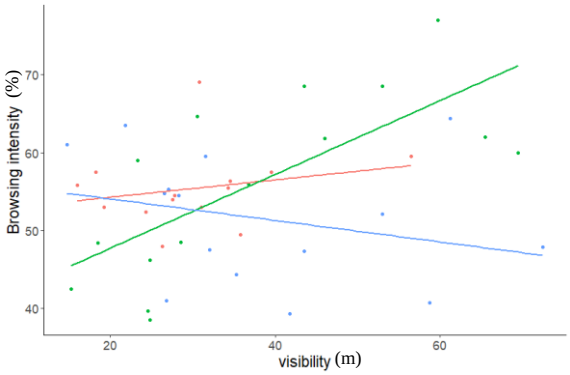

Figure 8. Percentage of top shoots damaged against horizontal visibility in different distance classes. Red - distance class 1, green - distance class 2, blue - distance class 3.

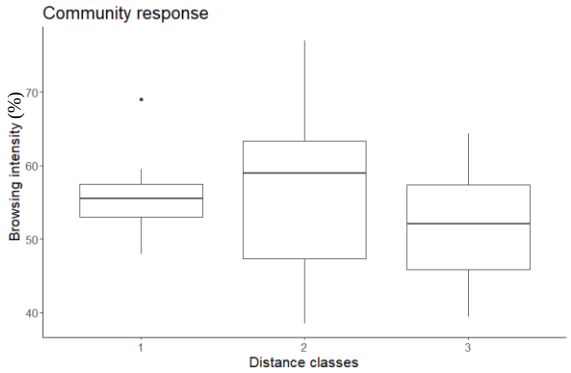

Figure 9. A boxplot of average percentage top shoots damaged in different distance classes.

Species response

Browsing intensity differed among species (p=0.0115). *T.cordata* was browsed less than other species grouped together (p=0.009) and slightly less than *C.betulus* (p=0.089) (fig.11). Browsing intensity in *C.betulus* was also explained by other ungulate biomass and distance interaction (other biomass x distance, p=0.026, F=5.449) (table 5). Browsing intensity on *C.betulus* follows the general trend of community-averaged responses, it increases with increasing ungulate biomass in distance class 2 but decreased in distance class

3. In a case of *A.platanoides* browsing intensity increased with browsing intensity (p=0.012, F=7.772). Variation within distance classes explained best with wolf density and distance interaction (wolf x distance, p=0.034, F=5.449) (table 5). Browsing intensity increased with increased of wolf density in distance class 1 and decreased in distance classes 2 and 3. Browsing intensity for other species differed between distance class 1 and 3 (p=0.048) (fig.10). The pattern through the distance classes was explained by wolf density (p=0.009) and red deer biomass (p=0.041).

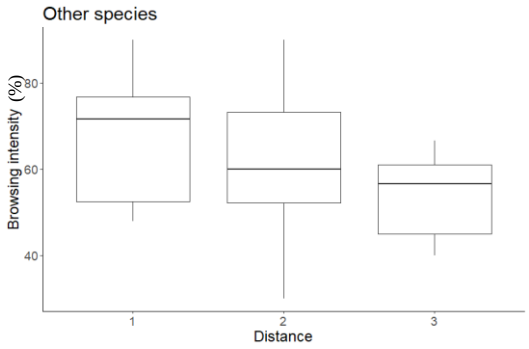

Figure 10. A boxplot of average percentage top shoots damaged of other species grouped together through distance classes.

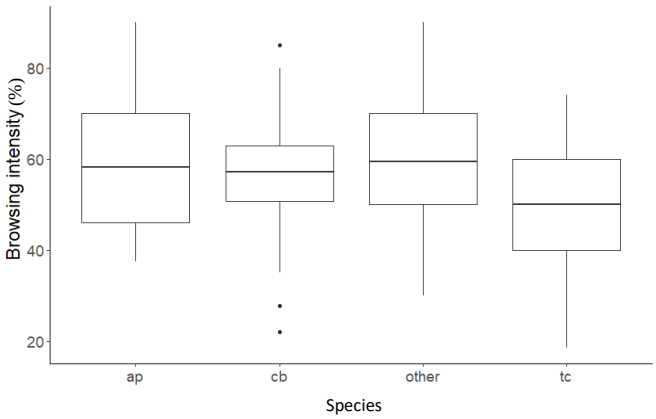

Figure 11. Boxplot with diameter-height index by four different species. Ap - Acer platanoides, cb – Carpinus betulus, other – all other species grouped together, tc – Tilia cordata

Height

Community-averaged response

Average sapling height did not vary across the distance classes (fig. 12). The variation within the distance classes in height was best explained by wolf density and red deer biomass variables in (table 3). Wolf density in an interaction with distance classes explained variation the best (wolf x distance, p=0.007, F=5.737) (table 3) (fig.13(top)). Average height increased with increased wolf density in distance classes 1 and 2 but decreases in distance class 3. The effect of red deer biomass also varied among distance classes (red deer biomass x distance, p=0.027, F=3.965) (table 3). While height increased with an increase of red deer biomass in distance classes 1 and 3, height decreased in distance class 2 (fig.13 (bottom)).

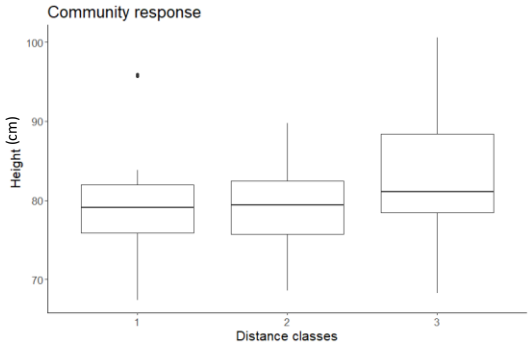

Figure 12. A boxplot of average tree heights in different distance classes (1 - the closest to human settlements, 3 - the furthest to human settlements)

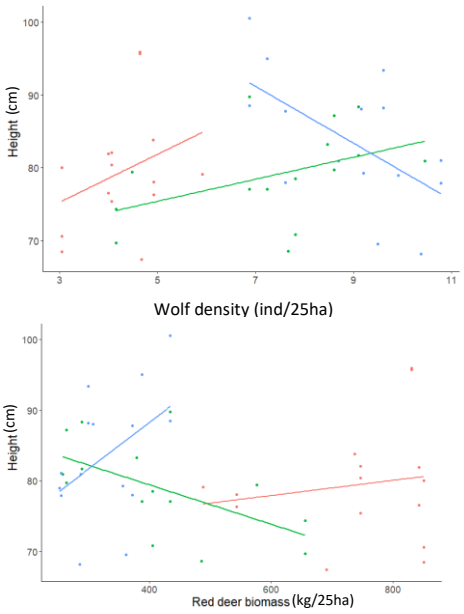

Figure 13. Height against relative wolf density (number of wolves) and red deer biomass in different distance classes. Red - distance class 1, green - distance class 2, blue - distance class 3

Species response

There was no difference in sapling height between the species (p=0.132) (fig.21). Variation in height within distance classes for *C.betulus* was best explained by relative wolf density, in distance classes 1 and 2 there is increase in height but in distance class 3 height decreases with relative wolf density (wolf x distance, p=0.01, F=5.22) (table 5). The variation was also explained by the red deer biomass in different distance classes (red deer biomass x distance, p=0.039, F=3.551) (table 5).

Height of the first branch

Community-averaged response

There was no difference in the height of the first branch between across distance classes (fig.22). However, variation within distance classes can be explained by red deer biomass and relative wolf density (red deer biomass x distance p=0.039, F=3.516; wolf x distance p=0.042, F=3.433) (table 3). With increasing red deer biomass the height of the first branch increased in all distance classes (figure 8 (top)), however the rate of increase differed in distance class 2 from the other ones. Meanwhile the relative wolf density

effect is not as straight forward. Distance interaction with relative wolf density indicates different patterns in all distance classes. While branch height increases in distance class 1, it decreases in distance class 2 and remains unchanged in distance class 3 (figure 8 (bottom)).

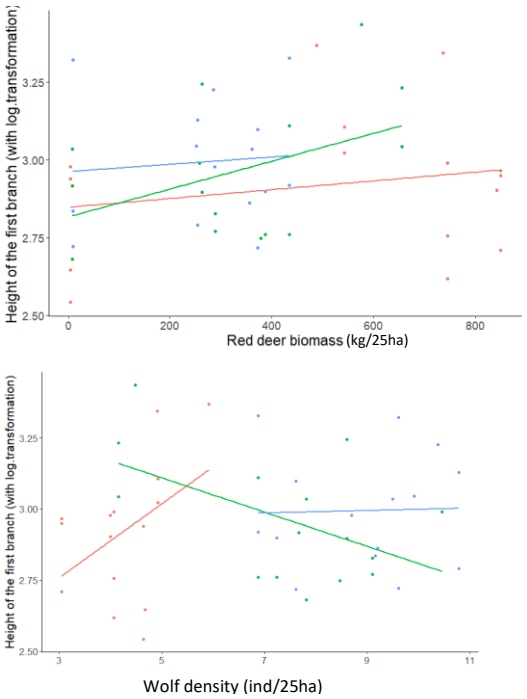

Figure 14. Height of the first branch against relative wolf density (ind/25 ha) and red deer biomass in different distance classes. Red - distance class 1, green - distance class 2, blue - distance class 3.

Species response

The height of the first branch differed between the species ($p<0.001$). *C.betulus* had the lowest first branch of 3 most abundant species and the other species grouped together ($p<0.001$) (fig.24). Looking at the species level, *C.betulus* had a consistently low first branch throughout the distance classes. However, none of my models could explain variation for *C.betulus.* Relative wolf density in different distance classes explained height of first branch in *T.cordata* the best (wolf x distance, $p=0.006$, $F=6.125$) (table 5). Distance classes 1 and 2 showed very similar pattern to community averaged response (fig.15), branch height increased with relative wolf density in distance class 1 and decreased in distance class 2. Red deer effect was also explained well

with an interaction with distance classes (red deer biomass x distance, p=0.01, F=5.467) (table 5).

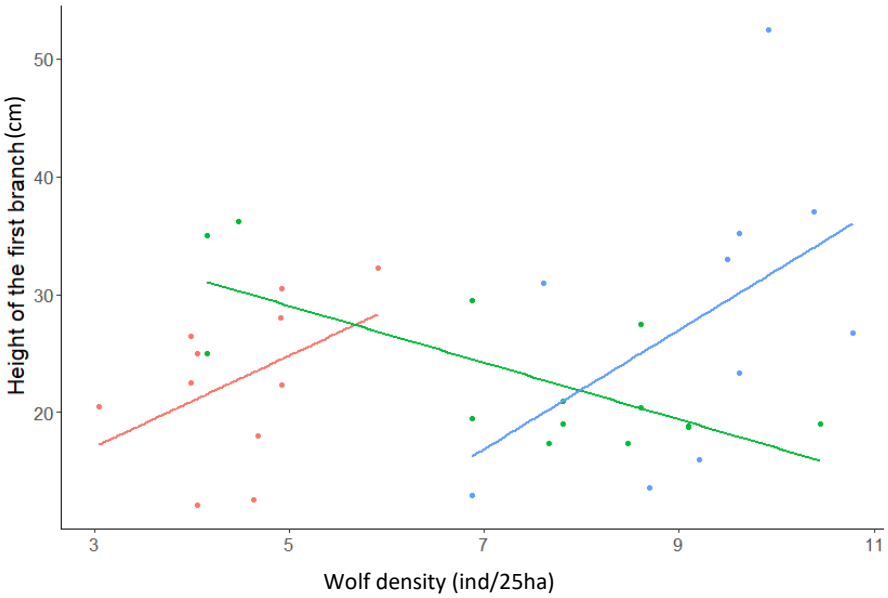

Figure 15. T.cordata response to against relative wolf density (ind/25 ha) in different distance classes. Red - distance class 1, green - distance class 2, blue - distance class 3.

Height of the first fork

Community-averaged response

There was no difference in the height of the first fork between difference distance classes. However, a model without an interaction showed that the height of the fork increases with increased other ungulate biomass (p=0.002, F=11.985) (fig.16)

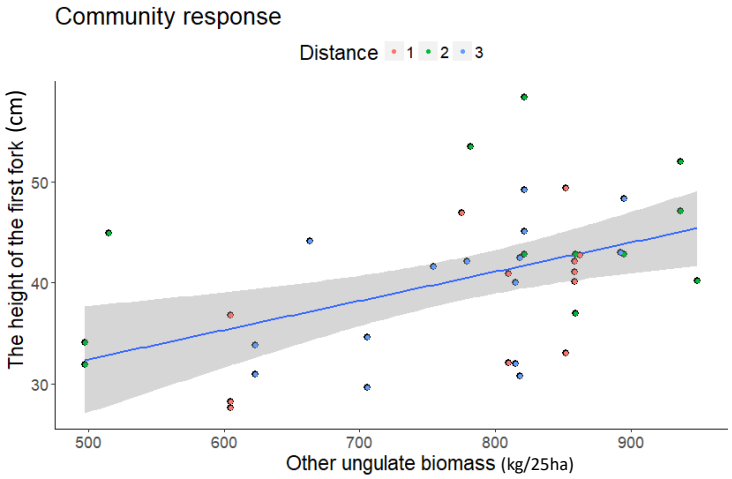

Figure 16. The height of the first fork in response to other ungulate biomass with 95% confidence interval.

Species response

There was no difference in the height of the fork among different species. Explanatory variables did not affect height of the first fork for any of the species ($p>0.079$).

Branching index

Community-averaged response

There was no difference in branching index between different distance classes (fig.24). Branching intensity was explain the best by browsing pressure ($p=0.002$, $F=10.734$). Branching index increased with increased browsing intensity ($r^2=18.12$) (fig.17) The variation within the distance classes was explained by an interaction between visibility and distance (visibility x distance, $p=0.042$, $F=3.454$) (table 3). While branching index steadily increased with increased visibility in distance classes 1 and 2, it decreases in distance class 3 (fig.18). In other words, trees become branchier with more horizontal visibility in distance classes 1 and 2. However

the effect becomes opposite and number of branches decreases per 1cm of height in distance class 3 in more horizontal visibility.

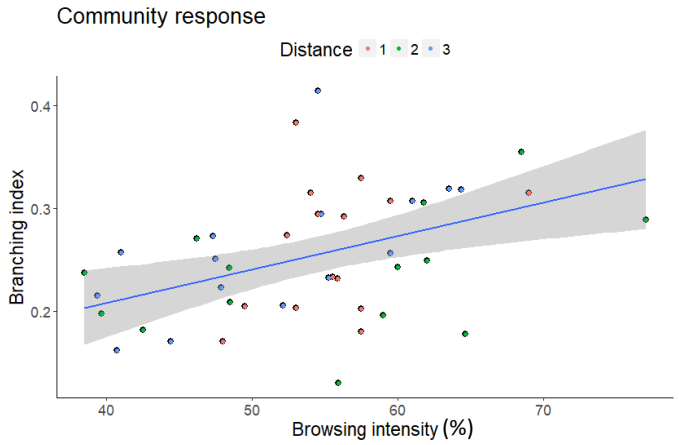

Figure 17. Linear regression between branching index and browsing intensity with 95% confidence interval.

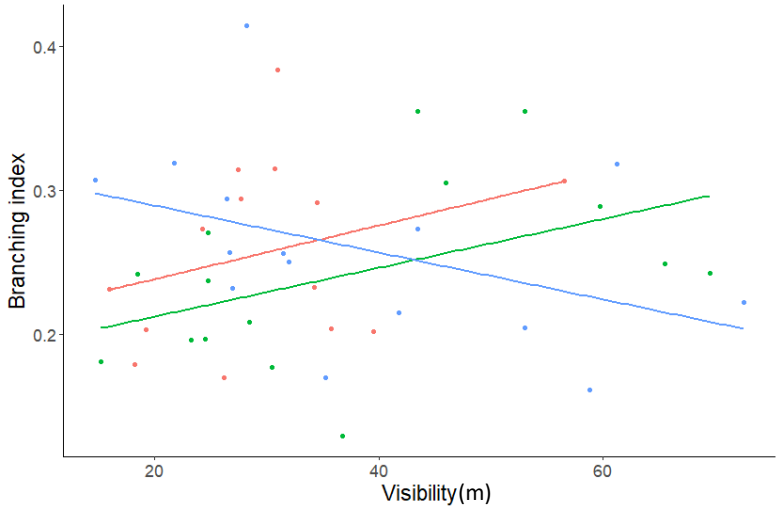

Figure 18. Branching index against visibility in different distance classes. Red - distance class 1, green - distance class 2, blue - distance class 3.

Species response

Three most abundant species and the other species grouped together had different average branching indices ($p<0.001$) (fig19). *C.betulus* had the highest branching index ($p<0.001$), followed by *T.cordata* which was different from all other species except *A.platanoides* (fig.19). *C.betulus*

branching index also increased with browsing intensity (p=0.008, F=7.741). *C.betulus* variation in branching index within distance classes was best explained by other ungulate biomass interaction with distance classes (other biomass x distance, p=0.012, F=4.935) (table 5). In this model with increasing other ungulate biomass branching index also increased in distance classes 1 and 2, but decreased in distance class 3 (fig.25). Branching index in *T.cordata* was best explained by an interaction between red deer biomass and visibility (red deer biomass x visibility, p=0.035, F=4.874) (table 5).

s

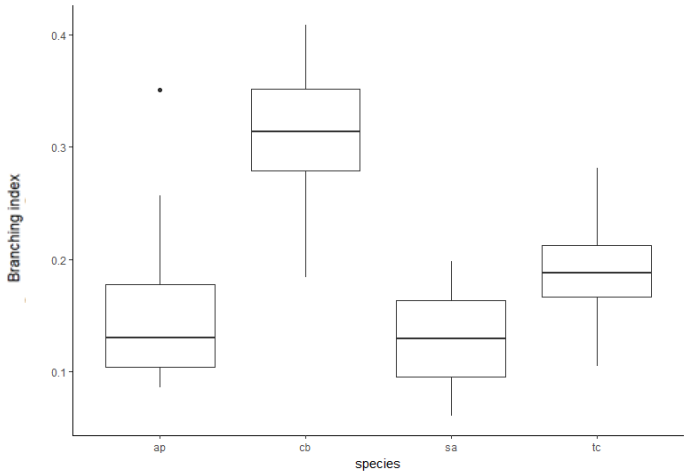

Figure 19. Boxplot for branching index in four different species. Ap - Acer platanoides, cb – Carpinus betulus, sa – Sorbus aucuparia, tc – Tilia cordata.

Diameter – height index

Community-averaged response

Diameter-height index did not change amongst distance classes (fig. 26). The only model that explained variation was other ungulate biomass in interaction with visibility (other biomass x visibility, p=0.043, F=4.383) (table 4). Diameter – height index showed an increased with both variables.

Species response

There was a difference in DH index between the species (p<0.001) (fig.27). *T.cordata* was the most different from other species with the highest

average DH (p<0.001). DH index in *T.cordata* also varied between distance classes (p=0.033). In distance class 3 *T.cordata* index was lower compared to distance class 2 (p=0.04) (fig.28). *C.betulus* was also different from *A.platanoides* (p<0.05). It also differed among distance classes (p=0.005). DH index was the highest in distance class 3 and lowest in distance class 1 (p=0.004). *C.betulus* showed a strong response to relative wolf density and distance class interaction (wolf x distance, p=0.005, F=6.191) (table 5). In this model DH index increases with an increase of relative wolf density in distance classes 1 and 2 but decreases in distance class 3 (fig.20). An interaction between other ungulate biomass and visibility also made a strong response in *C.betulus* DH index (other biomass x visibility, p=0.008, F=7.809)(table 5). DH index in *T.cordata* responded well to the distance but not so much to wolf density or ungulate biomass (table 5).

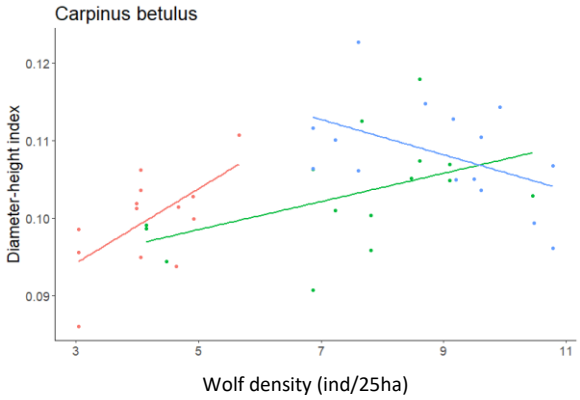

Figure 20. C.betulus DH index against relative wolf density in different distance classes. Red - distance class 1, green - distance class 2, blue - distance class 3.

Discussion

In my thesis first, I aimed to look at the effect that perceived risk from wolves has on browsing intensity of regenerating tree communities. To do so I related browsing intensity to red deer biomass, wolf density and horizontal visibility gradients in relation to the distance classes. Red deer biomass, indeed decreased with relative wold density In areas where relative wolf density is high and red deer biomass is low, however, browsing intensity persisted. In these areas with higher relative wolf density reduction in red deer browsing was compensated by changes in other ungulate biomass. Second, I examined the effect of perceived risk on several specific plant traits. Sapling height and the height of first fork related to red deer biomass and relative wolf density. Branching index related to visibility and diameter-height index related to visibility and other ungulate biomass. Analysis of browsing intensity and branching index revealed that red deer may not be the only browser species that influences tree architecture in BNP. As the risk effect did not affect other ungulates the same way as it did red deer, it also did not influence plant traits in regenerating tree communities.

One central assumption in my study was that relative wolf density increased with increasing distance from the village. As wolf density increased moving further away from the human settlements, red deer biomass decreased (fig.6). According to a previous study from Białowieża Primeval forest wolves are more likely to have denning sites further away from human settlements (Kuijper *et al*., 2015). In these wolf core areas, the risk for red deer to be predated upon increases 5 times (Kuijper *et al*., 2013). Since average biomass of red deer decreases by more than half in distance classes 2 and 3 (fig.6), red deer may still utilize high risk areas as a trade-off for high nutritional value reward (Abrams, 1984). At the same time the other ungulate biomass does not change throughout all distance classes (fig.6). Therefore, I conclude that red deer is affected by the risk of predation of wolves more than other ungulates.

Kuijper *et al* (2013) showed that red deer became more vigilant inside of wolf core area, especially when large downed logs were present. Such fine-scale risk factors reduced red deer browsing around fallen logs in 16 metre radius in high predation risk areas (van Ginkel *et al*., 2018). This, in theory, should allow trees to escape browsing a lot more in riskier areas. However, in my study I found that the average height of the saplings did not change throughout the distance classes. This could be tied to other ungulate browsing pressure in distance class 2 and, especially, 3, or, alternatively, to the fine-scale differences in productivity.

Out of three other browser species bison was encountered the most often, 61% of the time, roe deer 28% and moose 12% of the time (table 2) according to data from camera traps (Bubnicki *et al*., personal communication, 2018). This suggest that from the other ungulate species - bison are second most abundant browser species. Bison diet study suggested that non-supplementary fed bison can consume up to 65% of woody material (Kowalczyk *et al*., 2011), thus making them an important browser in a forest environment. I, therefore, strongly suspect that most of the browsing pressure, in distance class 3 and some parts of distance class 2, comes from bison. However, distance class 2 is a transitional area which may mean that red deer and bison occur in alongside and their numbers are highly variable from plot to plot.

Wolf diet in this system mainly consist of red deer and wild boar, rarely ever moose, roe deer or bison (Jędrzejewski *et al*., 2012). Thus, other browser species, except red deer, should not be affected as much or the same way by wolf presence and cues. Since data indicates that bison is the second most common browser species, bison may indeed, show lack of fear. That is also backed up as Jędrzejewski *et al*. (1992) who pointed out that there has not been any recorded wolf predation on bison in BNP. In this system red deer and bison may be competing for food resources (Kowalczyk *et al*., 2011). Wolf directly and indirectly reduces numbers of one competitor

species, thus, this may suggest that competitive release may be in play. By releasing the habitat from red deer, wolf may be opening it to bison.

Capturing overall branching architecture of the regenerating tree community and species was one of my main focuses in the study, as it may be an important trait representing tolerance (Charles-Dominique *et al*., 2017). There have been several different ways used to capture plant branching density (Perez-Harguindeguy *et al*., 2013; Charles-Dominique *et al*., 2017). However, most of methods described in scientific literature were too labour and time consuming to be carried out in the field. The design I used balanced the effort and captured rough branching density of a tree. Nevertheless, it responded to browsing intensity, and increased along the browsing intensity gradient (fig.17). The community-weighted branching index increased along horizontal visibility in distance classes 1 and 2 but decreased in distance class 3. One of my prediction is that red deer have tendency to avoid more visible areas and other ungulates, in this case bison, does not (fig.6). This may be the reason why browsing intensity increases with visibility, as it also increases alongside with other ungulate biomass in distance classes 1 and 2. However, other ungulate biomass, browsing intensity and branching index decrease with visibility in distance class 3. In the case of red deer, browsing intensity could have another interpretation. While, more horizontal visibility means mature forest with little undergrowth. Less visibility might represent, for example, a lot of undergrowth or large fallen tree. One of the explanations for browsing intensity could be that red deer avoid open areas due to predation risk (Laundré *et al*., 2001; Kuijper *et al*., 2015).

On a species level only *C.betulus* and *A.platanoides* branching index was explained by browsing intensity (fig.29, fig.30 in Appendix) indicating that not all species responded the same way to intensive browsing. Interestingly these two species are the opposites in their branching architecture strategies, where *C.betulus* is known to be capable of producing a "cage" architecture (Cromsigt and Kuijper, 2011) and *A.platanoides* generally is not expected to do so. Their branching architecture also indicates

that these species represent contrasting worlds, *C.betulus* being brown world species and *A.platanoides* – green world (Churski *et al*., 2016). In conditions where no browsers are present and in both high light and low light *A.platanoides* shows the largest height increment, however, even with browsing and low light conditions *C.betulus* manages to survive and escape browsing (Churski *et al*., 2016). It is highly suggestive that branching architecture helps *C.betulus* survive high browsing intensity long enough to escape browsing.

The only traits that responded to red deer biomass were sapling height and the height of the first branch. The effect of red deer biomass on these traits varied a lot depending where in the forest plants were. Interestingly, sapling height increased in distance classes 1 and 3. Whereas, in the distance class 2, where browsing pressure is slightly higher, sapling height decreases (fig.13). Some of the species of BNP may be able to compensate or overcompensate in growth under browsing. Several studies in different ecosystems showed compensatory growth in woody plants after an herbivory event (Aldous *et al*., 1952, du Toit *et al*., 1990; Edenius *et al*., 1993). None of the most common species indicated any strong increase when related to browsing intensity. However, compensatory growth does not explain an increase of sampling branch height in distance class 2. An interaction between distance classes and red deer biomass in response of sampling height and height of the first branch might have a threshold relationship, where general direction changes completely at around 20-24kg/ha (500-600kg in 25ha) (fig. 7 and fig.8). Even though, the interaction was not significant but the height of the first fork also suggests threshold effect against the red deer biomass (fig. 31 in Appendix).

Some species displayed more variation than the others, which may be tied with the ability to survive chronic browsing. It was interesting to look into the features that makes *C.betulus* such a successful species in closed canopy forest with high top-down control (Kuijper *et al*., 2010). *C.betulus* completely dominated the sapling communities I measured. It was

representing 45% to 57% of saplings in each distance class. From field observations the species was highly plastic, it developed both cage and pole structures depending on various factors. In the analysis it also had the lowest first branch from other species and had the highest branching index. The ability to do this in very limited light conditions must be one of its keys to succession. Both traits give *Carpinus* bushy shape which reduces the bite size of a browser (Charles-Dominique, *et al*., 2017). *C.betulus* was the only species observed in the closed canopy forest could develop classic "cage" structure. In BNP I have also observed *Carpinus* lawns, which are highly dense, highly browsed and highly branched trees occupying an area at least 5 metres by 5 metres in size. *C.betulus* was the main one species occurring, with occasional *T.cordata* or *A.platanoides* individual. Even though, *T.cordata* did not demonstrate clear "cage" structure, its average branching index was higher than other species grouped together. It also had the highest diameter-height index, which indicates that *T.cordata* is also able to persist with chronic browsing for a long time. *T.cordata* was second most common species in my study, occupying 10-35% of all distance classes. It seems like *T.cordata* as well as *C.betulus* both could be brown-world species. Contrarily, *A.platanoides* did not demonstrate any phenotypical traits that would allow tolerance to intensive browsing but its occurrence increased from 6% in distance class 2 to 12% in distance class 3. The increase is too small for difference between classes but the trend is observable. It may suggest that this is due to risk of predation by wolves. Outside of forest with unlimited light, several other species demonstrated clear "cage" architectural design (figures 34). They had such extreme "cage" structures that counting primary branches was impossible. Several *C.betulus*, *Prunus spp* and *T.cordata* were more wide than they were tall.

Distance classes were good basis for the experimental design. They gave a clear spatial frame to carry out in the field. However, during the analysis, I should have used a continuous distance from human settlement variable or a finer scale distance classes. As distance classes did not show any

difference from the start of analysis I should have tried different means of measuring distance from human settlements. During the data collection I should have also taken more extra notes especially on variables like visibility. Extra notes would have made it clearer what exactly was limiting horizontal visibility, whether it was a lot of regenerating trees or a large downed tree. Another additional data I should have collected is density of regenerating tree communities. It may have given an insight on browsing intensity and overall changes with ungulate biomass. It would have been interesting to see if browsing intensity increased with plant density. I also would have liked to compare data between open and closed forest canopy. As light gradient is more important for some species than other, it would have been interesting to compare change of plant traits for green-world species like *A.platanoides.* Due to the nature of the study I was forced to run many statistical tests, which increase the risk of type I error. Bonferroni correction can be used in such cases to counteract such problem. However, using the correction method the risk of type II error increases, thus I have decided to avoid it in this particular case.

In conclusion, my analysis demonstrated interesting patterns in plant trait formation under low light and high browsing conditions. As tree plant traits are rarely observed in a natural system with varying numbers and species of ungulates this can give an insight into certain patterns that may occur. The risk factor for red deer was almost overruled by browsing of European bison. Wolves have helped make this possible by directly and indirectly controlling red deer numbers further away from human settlements. Without the risk factor this habitat would not have been as open for bison to establish. Additionally, I have deducted that bison might not only use forest as refuge but actively feed and make an impact on regenerating trees. Predation risk has impacted how plant traits form, as one browser was replaced by another. However, the risk factor still made an impact on the ecosystem.

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Appendix

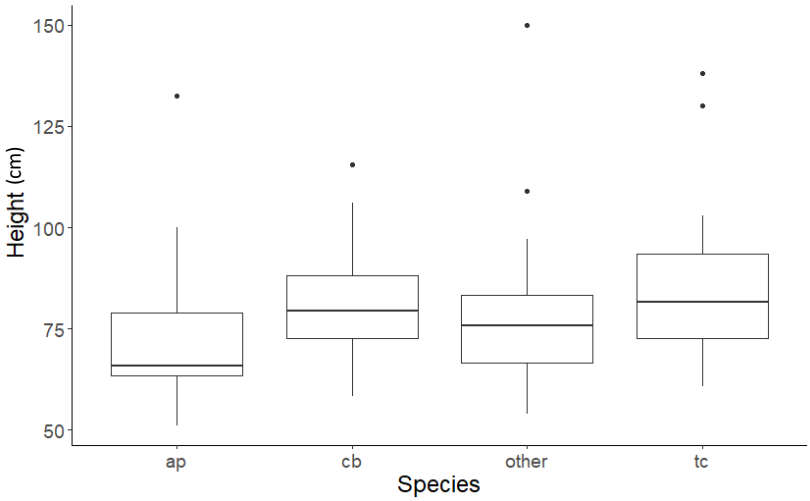

Figure 21. Boxplot for heigh in four different species. Ap - Acer platanoides, cb – Carpinus betulus, other – the other species averaged together, tc – Tilia cordata.

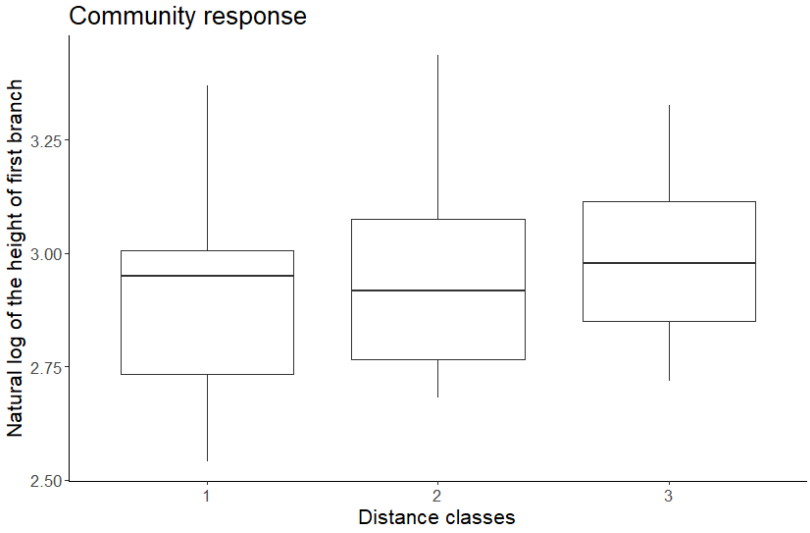

Figure 22. Boxplot for the height of the first branch in three different distance classes.

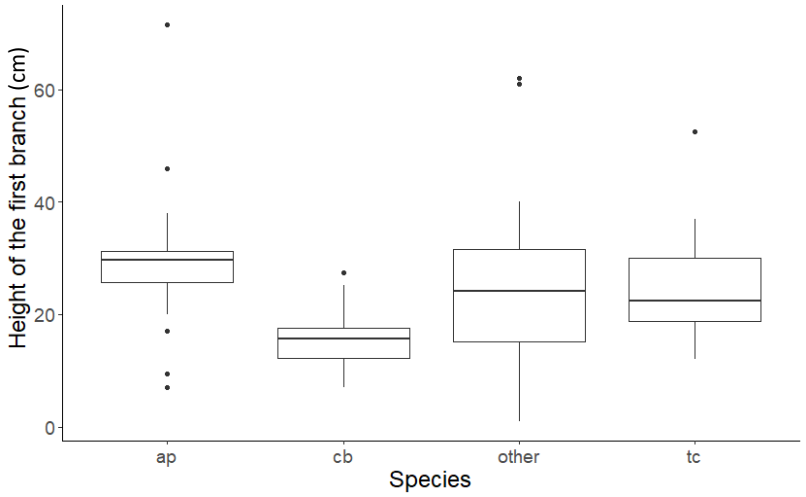

Figure 23. Boxplot for the heigh of the first branch in four different species. Ap - Acer platanoides, cb – Carpinus betulus, other - the other species averaged together, tc – Tilia cordata.

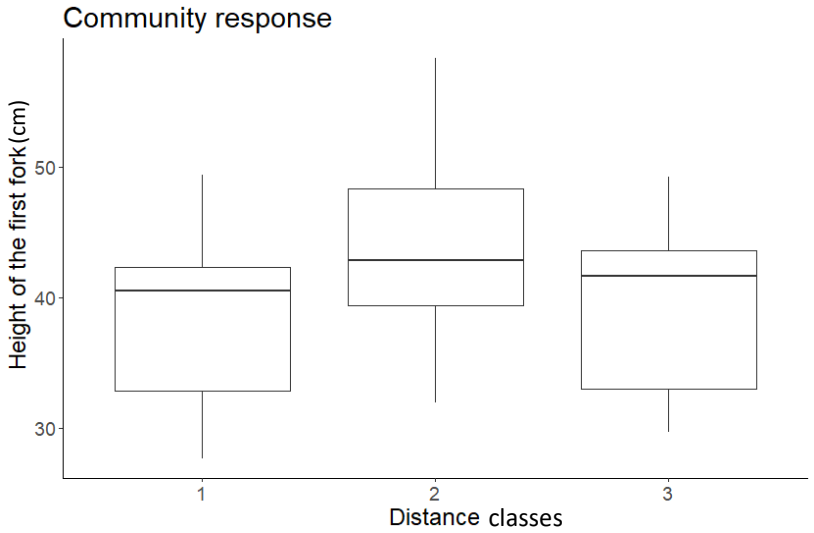

Figure 24. Boxplot for the height of the first fork in three different distance classes.

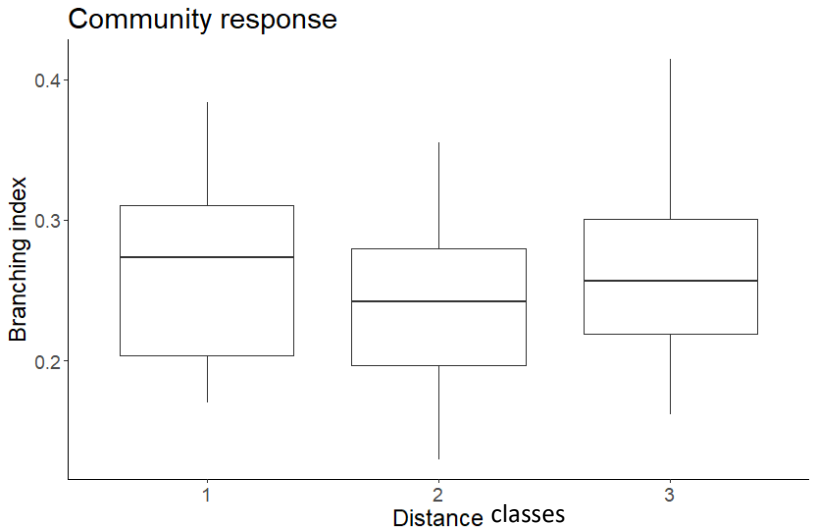

Figure 24. Boxplot for the height of branching index in three different distance classes.

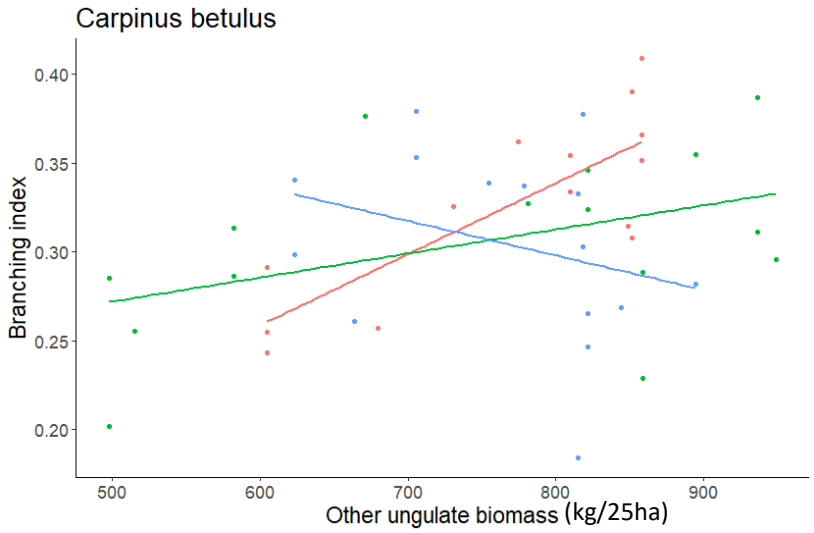

Figure 25. Branching index against other ungulate biomass different distance classes for C.betulus. Red - distance class 1, green - distance class 2, blue - distance class 3.6

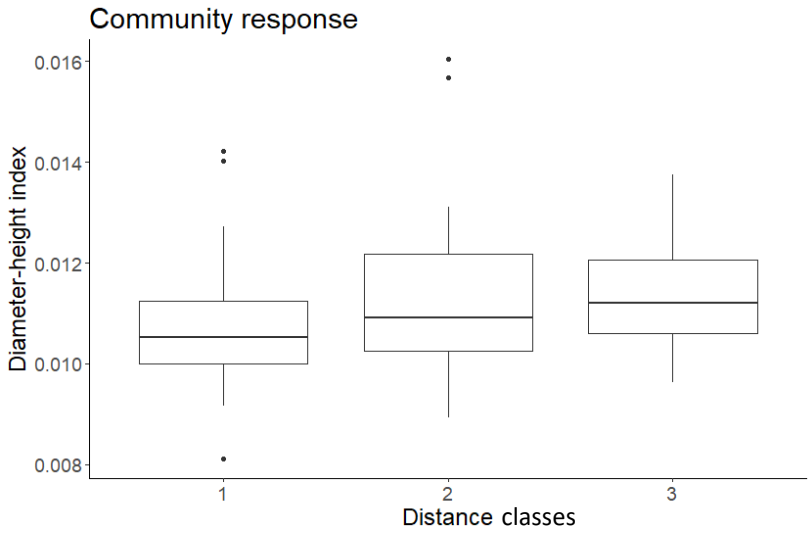

Figure 26. Boxplot for the height of diameter-height index in three different distance classes.

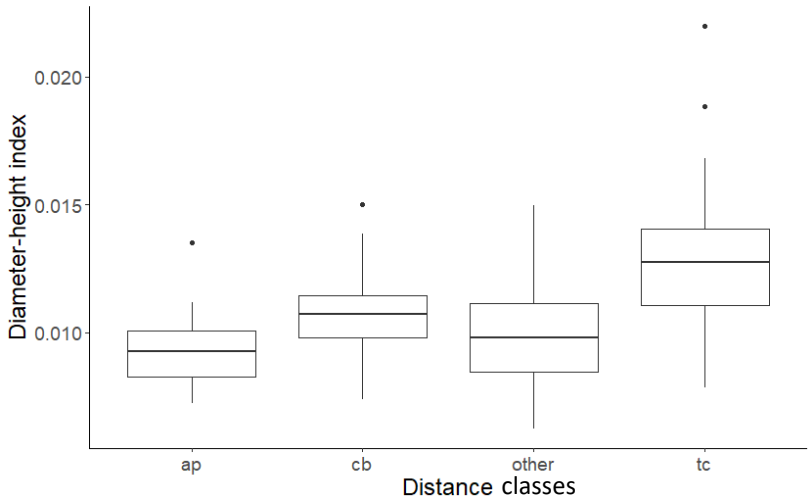

Figure 27. Boxplot for the heigh of the first branch in four different species. Ap - Acer platanoides, cb – Carpinus betulus, , other - the other species averaged together, tc – Tilia cordata.

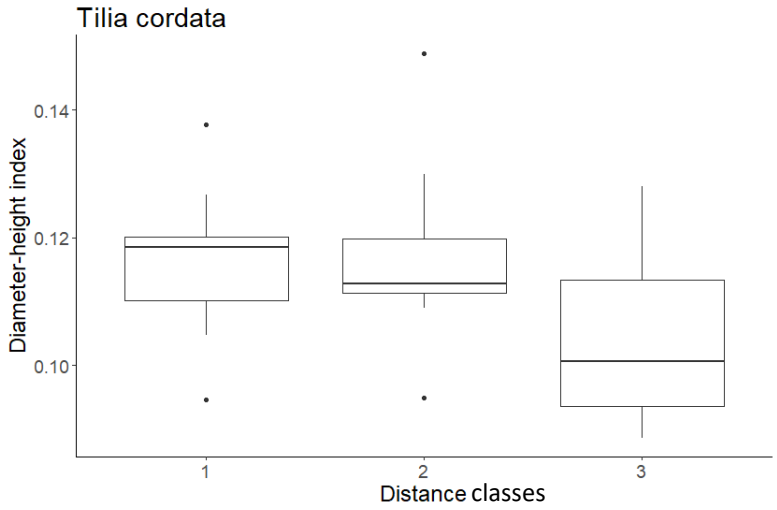

Figure 28. Boxplot for the height of diameter-height index in three different distance classes

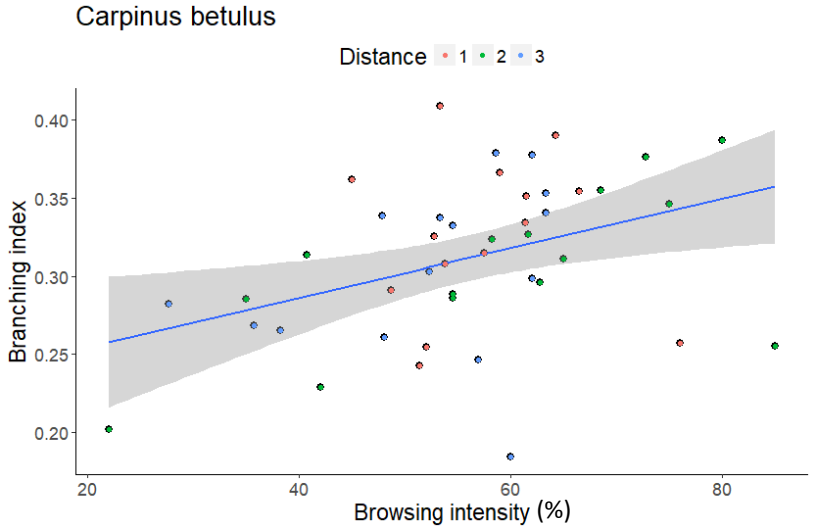

Figure 29. A linear regression of branching index against browsing intensity for C.betulus. Different colour respresents different distance classes.

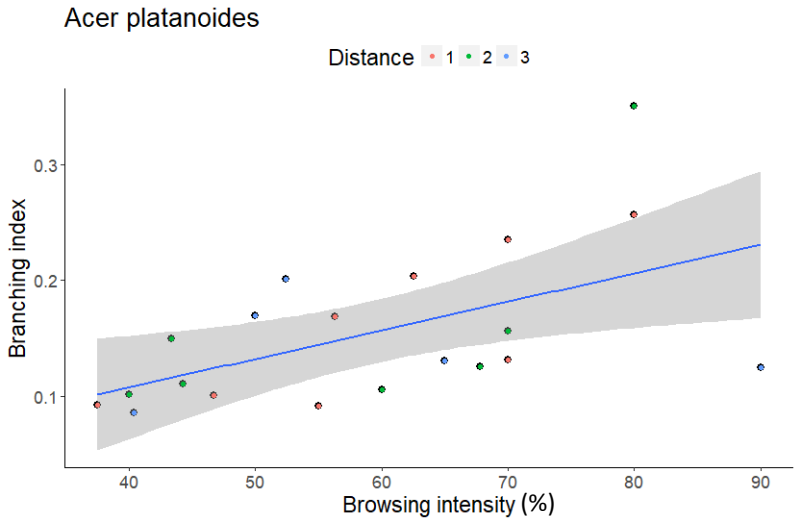

Figure 30. A linear regression of branching index against browsing intensity for C.betulus. Different colour respresents different distance classes.

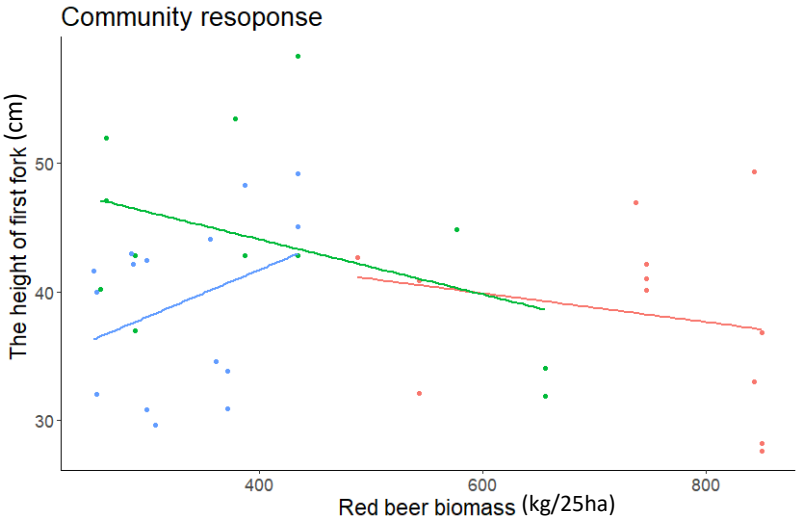

Figure 31. The height of the firdt fork against redndeer biomass in different distance classes for C.betulus. Red - distance class 1, green - distance class 2, blue - distance class 3.

Figure 34. 2 metre telescopic stick indicates width and height of extremely branched Carpinus betulus. The width of this individual was almost 200cm and height was just over 150cm

Table 3 (was 2). Community-averaged GLM's for all plant traits against continuous variables and distance class.

Plant trait	Explanatory variable	Df	F-value	P-value	Estimates	AIC
Height	Wolf	1	1.270	0.267	3.29	
	Distance	2	1.215	0.308	27.712	
	Wolf:distance	2	5.737	**0.007**	-4.481	314.1
	Red deer biomass	1	1.123	0.296	0.011	
	Distance	2	1.181	0.318	4.76	
	Red deer biomass:distance	2	3.965	**0.027**	0.008	317.34
	Total biomass	1	0.030	0.863	0.015	
	Distance	2	4.062	**0.025**	-13.34	
	Total biomass:distance	2	0.523	0.597	0.0185	319.36
	Other biomass	1	4.094	0.050		
	Distance	2	1.383	0.263		
	Other biomass:distance	2	0.374	0.690		320.87
	Visibility	1	2.411	0.129		
	Distance	3	2.060	0.142		
	Visibility:distance	3	2.582	0.089		310.8
Branch	Wolf	1	0.063	0.803	0.13	
	Distance	2	0.782	0.465	0.813	
	Wolf:distance	2	3.433	**0.042**	-0.158	-5.2489
	Red deer biomass	1	0.710	0.405	-9.00E-04	
	Distance	2	0.085	0.919	-0.8005	
	Red deer biomass:distance	2	3.516	**0.039**	0.0015	-4.6948
	Total biomass	1	0.800	0.376		
	Distance	2	0.041	0.960		
	Total biomass:distance	2	1.154	0.326		0.07778
	Other biomass	1	0.017	0.897		
	Distance	2	0.404	0.671		
	Other biomass:distance	2	2.039	0.144		-1.712
	Visibility	1	0.559	0.459		
	Distance	3	0.281	0.756		
	Visibility:distance	3	0.952	0.395		1.458
Fork	Wolf	1	0.897	0.351		
	Distance	2	2.241	0.122		
	Wolf:distance	2	2.597	0.090		268.27
	Red deer biomass	1	1.743	0.196		
	Distance	2	1.991	0.153		
	Red deer biomass:distance	2	1.510	0.236		269.94
	Total biomass	1	0.321	0.575		
	Distance	2	6.218	0.005		
	Total biomass:distance	2	0.849	0.437		264.94
	Other biomass	1	11.985	**0.002**	4.00E-02	
	Distance	2	2.599	0.090	11.144	
	Other biomass:distance	2	0.663	0.522	-0.01	261.74
	Visibility	1	1.363	0.252		
	Distance	2	1.568	0.224		
	Visibility:distance	2	0.186	0.831		266.86
Branching index	Wolf	1	0.021	0.886		
	Distance	2	0.401	0.673		
	Wolf:distance	2	0.431	0.653		-109.37
	Red deer biomass	1	0.047	0.829		
	Distance	2	0.936	0.401		
	Red deer biomass:distance	2	0.007	0.993		-109.64
	Total biomass	1	0.644	0.427		
	Distance	2	0.486	0.619		
	Total biomass:distance	2	1.898	0.164		-113.31
	Other biomass	1	3.229	0.080		
	Distance	2	0.363	0.698		
	Other biomass:distance	2	2.658	0.083		-117.06
	Visibility	1	0.296	0.589	0.201	
	Distance	2	0.403	0.671	0.072	
	Visibility:distance	2	3.454	**0.042**	-0.002	-113.62

Diameter-height index	Wolf	1	2.094	0.156		
	Distance	2	0.175	0.840		
	Wolf:distance	2	2.130	0.133		-304.04
	Red deer biomass	1	3.682	0.062		
	Distance	2	0.548	0.583		
	Red deer biomass:distance	2	0.705	0.500		-303.53
	Total biomass	1	0.738	0.396		
	Distance	2	0.343	0.712		
	Total biomass:distance	2	0.493	0.615		-299.6
	Other biomass	1	3.390	0.073		
	Distance	2	0.871	0.426		
	Other biomass:distance	2	2.120	0.134		-306.6
	Visibility	1	0.359	0.553		
	Distance	2	0.913	0.410		
	Visibility:distance	2	1.086	0.348		-293.81
Browsing intensity	Wolf	1	0.439	0.511		
	Distance	2	0.951	0.395		
	Wolf:distance	2	0.048	0.953		333.15
	Red deer biomass	1	0.005	0.942		
	Distance	2	2.011	0.148		
	Red deer biomass:distance	2	0.034	0.967		331.39
	Total biomass	1	0.634	0.431		
	Distance	2	1.115	0.338		
	Total biomass:distance	2	5.249	**0.010**		322.62
	Other biomass	1	1.263	0.268		
	Distance	2	1.402	0.258		
	Other biomass:distance	2	1.812	0.177		327.78
	Visibility	1	4.193	**0.048**	0.473	
	Distance	2	2.159	0.129	16.14	
	Visibility:distance	2	6.827	**0.003**	-0.487	309.37

Table 4. Community-averaged GLM's for all plant traits in interaction between continuous variables and visibility.

Plant trait	Explanatory variable	Df	F-value	P-value	Estimates	AIC
Height	Wolf	1	0.914	0.345		312.81
	Visibility	1	3.315	0.076		
	Wolf:visibility	1	1.400	0.244		
	Red deer biomass	1	0.792	0.379		314.36
	Visibility	1	3.183	0.082		
	Red deer biomass:visibility	1	0.074	0.787		
	Total biomass	1	0.122	0.728		316.15
	Visibility	1	1.949	0.170		
	Total biomass:visibility	1	0.225	0.638		
	Other biomass	1	4.694	0.036	0.036	309.33
	Visibility	1	4.423	**0.042**	0.088	
	Other biomass:visibility	1	0.273	0.604	-0.0003	
Branch	Wolf	1	0.063	0.803		0.22079
	Visibility	1	0.492	0.487		
	Wolf: visibility	1	0.001	0.973		
	Red deer biomass	1	0.698	0.409		-
	Visibility	1	0.285	0.596		
	Red deer biomass: visibility	1	0.010	0.922		
	Total biomass	1	0.943	0.337		-1.1316
	Visibility	1	0.380	0.541		
	Total biomass: visibility	1	0.499	0.484		
	Other biomass	1	0.019	0.892		-
	Visibility	1	0.642	0.428		
	Other biomass: visibility	1	0.450	0.506		
Fork	Wolf	1	0.478	0.494		265.82
	Visibility	1	1.029	0.318		
	Wolf: visibility	1	0.729	0.399		
	Red deer biomass	1	0.999	0.325		265.86
	Visibility	1	0.881	0.355		
	Red deer biomass: visibility	1	0.324	0.573		
	Total biomass	1	0.876	0.356		264.88
	Visibility	1	1.780	0.191		
	Total biomass: visibility	1	0.494	0.487		
	Other biomass	1	12.128	0.001		256.03
	Visibility	1	0.569	0.456		
	Other biomass: visibility	1	0.192	0.664		
Branching index	Wolf	1	0.005	0.946		-113.17
	Visibility	1	0.284	0.597		
	Wolf: visibility	1	3.486	0.069		
	Red deer biomass	1	0.289	0.594		-111.46
	Visibility	1	0.148	0.702		
	Red deer biomass: visibility	1	1.668	0.204		
	Total biomass	1	0.186	0.669		-111.01
	Visibility	1	0.347	0.559		
	Total biomass: visibility	1	1.139	0.292		
	Other biomass	1	2.553	0.118		-112.33
	Visibility	1	0.027	0.872		
	Other biomass: visibility	1	0.363	0.551		

Diameter-Height index	Wolf	1	2.039	0.161		-298.13
	Visibility	1	1.101	0.300		
	Wolf: visibility	1	1.768	0.191		
	Red deer biomass	1	3.867	0.056		-299.64
	Visibility	1	1.512	0.226		
	Red deer biomass: visibility	1	1.101	0.300		
	Total biomass	1	0.725	0.400		-294.46
	Visibility	1	0.529	0.471		
	Total biomass: visibility	1	0.065	0.800		
	Other biomass	1	0.417	0.522	6.28E-05	-302.13
	Visibility	1	4.386	**0.042**	6.28E-05	
	Other biomass: visibility	1	4.383	**0.043**	-1.24E-06	
Browsing intensity	Wolf	1	0.416	0.523		319.16
	Visibility	1	4.212	0.047		
	Wolf: visibility	1	1.664	0.205		
	Red deer biomass	1	0.000	0.986		322.05
	Visibility	1	3.261	0.078		
	Red deer biomass: visibility	1	0.083	0.775		
	Total biomass	1	0.423	0.519		321.17
	Visibility	1	3.511	0.068		
	Total biomass: visibility	1	0.290	0.593		
	Other biomass	1	1.112	0.298		321.73
	Visibility	1	2.381	0.131		
	Other biomass: visibility	1	0.166	0.686		

Table 5. Species specific GLM's for all plant traits against continuous variable and distance class.

Plant trait	Species	Explanatory variable	Df	F-value	P-value	Estimates	AIC
Height	*Carpinus betulus*	Wolf	1	0.064	0.802	-0.088	342.87
		Distance	2	2.056	0.142	32.63	
		Wolf:distance	2	5.220	**0.010**	-3.333	
		Red deer biomass	1	0.153	0.698	0.006	348.24
		Distance	2	0.661	0.522	-9.98	
		Red deer biomass:distance	2	3.551	**0.039**	0.046	
	Tilia cordata	Visibility	1	0.164	0.689		297.75
		Distance	1	0.353	0.557		
		Visibility:distance	1	3.628	0.066		
	Other species	Wolf	1	0.418	0.523	23.129	299.03
		Distance	2	0.239	0.789	92.9275	
		Wolf:distance	2	3.779	**0.035**	-23.01	
		Red deer biomass	1	2.364	0.135	-0.254	285.14
		Distance	2	3.935	**0.031**	-197.537	
		Red deer biomass:distance	2	8.303	**0.001**	0.248	
		Total biomass	1	1.027	0.32		
		Distance	2	1.322	0.283		

		Total biomass:distance	2	2.699	0.085		
Branch	*Carpinus betulus*	Wolf	1	0.786	0.381		249.51
		Visibility	1	0.559	0.459		
		Wolf:visibility	1	3.711	0.061		
		Red deer biomass	1	0.781	0.382	0.018	249.79
		Visibility	1	0.219	0.642	0.271	
		Red deer biomass:visibility	1	3.764	0.060	-0.0006	
Branch	*Tilia cordata*	Wolf	1	0.730	0.400	3.871	247.92
		Distance	2	1.450	0.251	4.822	
		Wolf:distance	2	6.125	**0.006**	-2.5465	
		Red deer biomass	1	1.222	0.278	-0.025	249.26
		Distance	2	1.020	0.373	-3.74	
		Red deer biomass:distance	2	5.467	**0.010**	-0.0145	
Branch	Other species	Red deer biomass	1	0.455	0.506	-0.119	275.65
		Distance	2	0.12	0.887	-108.206	
		Red deer biomass:distance	2	4.837	**0.016**	0.166	
Fork	*Tilia cordata*	Other biomass	1	0.127	0.724		
		Visibility	1	1.414	0.246		
		Other biomass:visibility	1	3.342	0.079		
Branching index	*Carpinus betulus*	Other biomass	1	6.530	0.015	0.0004	-139.9
		Distance	2	0.887	0.420	0.3095	
		Other biomass:distance	2	4.935	**0.012**	-0.0005	
	Tilia cord.	Red deer biomass	1	1.434	0.240	7.77E-05	-120.66
		Visibility	1	4.874	**0.035**	7.13E+04	
Diameter-height index	*Carpinus betulus*	Wolf	1	13.742	**0.0007**	0.0048	-312.1
		Distance	2	1.632	0.209	0.0295	
		Wolf:distance	2	6.191	**0.005**	-0.005	
		Red deer biomass	1	16.176	**0.0003**	-3.08E-05	
		Distance	2	1.681	0.200	-0.016541	-308.2
		Red deer biomass:distance	2	2.036	0.145	3.14E-05	
		Other biomass	1	5.672	0.022		-311
		Distance	2	7.345	0.002		
		Other biomass:distance	2	3.702	0.034		
		Visibility	1	0.000	0.983		-293.1
		Distance	2	6.086	**0.005**		
		Visibility:distance	2	1.060	0.357		
		Wolf	1	0.000	0.983		-295.6
		Visibility	1	11.421	**0.002**		
		Wolf:visibility	1	1.774	0.191		
		Red deer biomass	1	0.001	0.983		-299.3
		Visibility	1	16.608	**0.0002**		
		Red deer biomass:visibility	1	1.356	0.251		
		Other biomass	1	0.000	0.983		-295.1
		Visibility	1	4.847	**0.034**		
		Other biomass:visibility	1	7.809	**0.008**		
	Tilia cordata	Other biomass	1	1.754	0.196		-200.9
		Distance	2	4.013	**0.029**		
		Other biomass:distance	2	0.430	0.655		
		Visibility	1	0.003	0.960	1.28E-04	-192.1

Browsing intensity	*Carpinus betulus*	Distance	2	3.451	**0.046**		
		Visibility:distance	2	0.679	0.515		
		Other biomass	1	1.661	0.205	-0.0007	350.75
		Distance	2	1.262	0.295	-0.0001	
		Other biomass:distance	2	4.005	**0.026**		
	Acer platan.	Wolf	1	0.508	0.487		159.77
		Visibility	1	0.089	0.770		
		Wolf:visibility	1	5.449	**0.034**	7.93	
	Other species	Wolf	1	7.345	**0.011**	1.375	284.28
		Distance	2	0.278	0.759	-0.196	
		Wolf:distance	2	0.859	0.434	-9.216	
		Red deer biomass	1	4.334	**0.047**	-35.165	286.82
		Distance	2	0.792	0.463	7.612	
		Red deer biomass:distance	2	0.494	0.615	-0.037	
		Total ungulate biomass	1	6.078	**0.02**	-48.364	278.12
		Distance	2	1.048	0.364	0.0585	
		Total ungulate biomass:distance	2	4.461	**0.021**	-0.056	

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